NEW STROPHALOSIIDAE (BRACHIOPODA) FROM THE EARLY PERMIAN OF ARGENTINA

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New representatives of the family Strophalosiidae (Brachiopoda) are described from the Tupe Formation of the Paganzo Basin, Argentina. The genus *Coronalosia* Waterhouse & Gupta is reviewed and the new taxa *Coronalosia argentinensis* sp. nov. and *Tupelosia paganzoensis* gen. et sp. nov. proposed. The age of the Tupe Formation is reviewed and a middle to late Asselian (Early Permian) age is preferred.

The new genus *Guadalupelosia* from the mid-Permian of West Texas, USA, is also proposed.

Key words: Permian, Argentina, Brachiopoda, Strophalosiidae, Paganzo Basin, West Texas, new taxa.

STROPHALOSIID brachiopods (Family Strophalosiidae) are a significant component of many Permian marine benthonic communities. The family underwent significant evolutionary expansion in areas of cold and temperate marine waters during the Permian (Waterhouse 1967). Strophalosiids, frequently of large size, were abundant throughout the Permian of Gondwana as indicated by the following regions and representative studies: New Zealand (Waterhouse 1964, 1982), eastern Australia (Briggs 1998; Waterhouse 1986), Western Australia (Archbold 1986, 1987, 1993), Irian Jaya (Archbold 1992), Tibet and the Himalaya (Zhang & Ching 1976; Waterhouse 1978; Waterhouse & Gupta 1978), Peninsular India (Archbold et al. 1996), the Salt Range, Pakistan (Waagen 1883) and Oman (Angiolini et al. 1997). Etheridge (1872) was the first to illustrate strophalosiids from the Permian of Gondwana when describing Sir Richard Daintree's Queensland palaeontological collections.

Strophalosiid brachiopods are also well developed in the younger Permian deposits of northeastern Siberia including the Kolyma region (Tolmachev 1912; Likharev 1932, 1934; Tsaregradskii 1945; Zavodovskiy 1960; Zavodovskiy & Stepanov 1971), the Verkhoyansk Mountains, including the Kharaulakh Range in the north (Fredericks 1931; Kashirtsev 1955, 1959; Abramov & Grigor'eva 1988; Solomina 1988), the Taimyr Peninsula (Ustritskiy & Chernyak 1963) and the Canadian Arctic (Waterhouse 1969). Somewhat rarer and often smaller forms are known from Novaya Zemlya (Kalashnikov & Ustritskiy 1981) the Kanin Peninsula, the northern Urals and the Pay Khoy (Kalashnikov 1993) perhaps reflecting warmer (temperate) marine temperatures. The same applies to transitional (temperate) faunas of the Russian Far East (Frederieks 1925) and north-east China (Lee et al. 1980). Strophalosiids are also smaller and rarer in peripheral Gondwanan regions (eg. Oman, the Salt Range and Peninsular Thailand) also reflecting somewhat warmer water temperatures (Angiolini et al. 1997; Waagen 1883; Grant 1976).

Tropical and subtropical Permian seas were characterised by small, usually rare strophalosiids as in regions such as the Zechstein Basin of Europe (Geinitz 1848) and the Glass Mountains of Texas (Cooper & Grant 1975). The family is apparently absent from the tropical faunas of South China.

SOUTH AMERICAN PERMIAN STROPHALOSIIDAE

The South American Permian marine faunas have yielded few strophalosiids. The family is absent in the classic Early Permian faunas of Bolivia and Peru (Kozlowski 1914; Branisa 1965; Newell et al. 1949) and has not been recorded from the mid-Permian of Venezuela (Hoover 1981). From Argentina, Antelo (1972; see also Amos 1979) described and figured a strophalosiid species from the Quebrada Larga, in the upper valley of the Rio Blanco, San Juan Province. He referred his specimens to the species *Strophalosia cornelliana*

Derby (1872), a species placed in *Heteralosia* King (1938) by Mendes (1959, 1961) and Antelo (1972), that was originally described from the Upper Carboniferous (Pennsylvanian) Itaituba Series, Amazon Basin, Brazil. As discussed below, Antelo's material is not closely related to Derby's species but is closely allied to *Coronalosia argentinensis* sp. nov. Antelo's (1972) described fauna shares species with the fauna of the Tupe Formation (Paganzo Basin) which has yielded the species described herein. This argues for a correlation of the two faunas (Simanauskas & Cisterna 2000a).

New records from Argentina

Stratigraphy and location. All specimens described herein come from outcrops of the Tupe Formation at La Herradura Creek, located on the western flank of Perico Hill, about 20 km northeast of Jachal, San Juan Province, Argentina (Fig. 1). This region belongs to the precordilleran or western sector of the Paganzo Basin (Guandacol Embayment). The Tupe Formation at this locality represents a brief but widely extended marine transgression from the Panthalassic Ocean into the western Paganzo Basin (Lopez Gamundi et al. 1994).

The brachiopods documented herein come from a 40 m thick marine interval in the upper part of the Tupe Formation, the lithologies of which consists of alternating sandstones, claystone and calcareous beds. The marine interval represents a short-lived marine transgression within a deltaic system with swamps and hence a high proportion of organic matter (Ottone & Azcuy 1986). All the strophalosiid specimens figured and described herein, come from an horizon approximately 25 m above the base of the marine interval (Fig. 2).

Previous studies and age. The stratigraphical section of the Tupe Formation at La Herradura Creek is considered to be the stratotype of the *Tivertonia jachalensis–Streptorhynchus inaequiornatus* Biozone (Sabattini et al. 1990). However, the brachiopod fauna of the Tupe Formation has been poorly understood in modern terms. Leanza (1945) described and illustrated several brachiopod species with the names *Chonetes scitula* Leanza, *Streptorhynchus inaequiornatus* Leanza, *Spirifer (Spirifer) pericoensis* Leanza and *Syringothyris keideli* Harrington. *Chonetes scitula* Leanza was later found to be a preoccupied name (Amos 1961) and was renamed as *Lissochonetes jachalensis* Amos. Simanauskas (1991) revised the species and included material from La Herradura Creek in his review.

Fig. 1. Location maps showing: A, South America; B, Argentina; C, San Juan Province; D, the Tupe Formation locality.

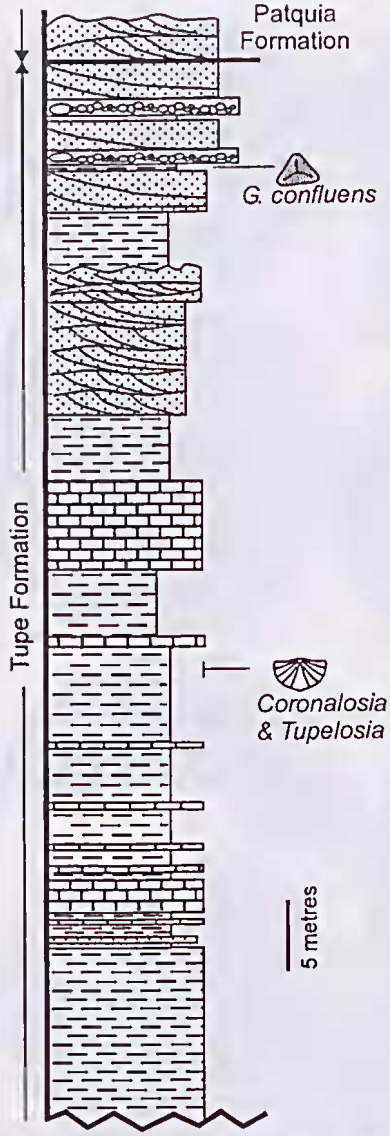


Fig. 2. Stratigraphical log of the upper part of the Tupe Formation, La Herradura Creek.

The *Tivertonia jachalensis–Streptorhynchus inaequiornatus* Biozone was previously known as the 'fauna intermedia' of Gonzalez (1985) and the 'Zona de Intervalo' of Archangelsky et al. (1987) who regarded the zone as being of Late Carboniferous age. More recent studies, which compare correlated Argentine faunas closely with other Gondwanan faunas and associated palynological data, point to an Early Permian (mid to late Asselian) age for the Zone (Cisterna & Simanauskas 2000; Simanauskas & Cisterna 2000b). These studies are consistent with Australian studies (eg. Archbold & Hogeboom 2000) that treat the first appearance datum of the spore *Granulatisporites confluens* as being of latest Asselian age. The Tupe Formation marine fauna occurs immediately below this key palynological zone and hence is regarded as being mid to late Asselian in age.

Collections. All figured specimens are housed in the collections of the Departimento Cientifico de Geologia, Museo de La Plata, with the registration prefix DCG-MLP. All figure specimens of new species, other than holotypes, are paratypes. Additional, fragmentary specimens of both new Argentinian species described herein were also examined.

SYSTEMATIC PALAEONTOLOGY

Order PRODUCTIDA
Sarycheva & Sokolskaya, 1959

Suborder STROPHALOSIIDINA
Waterhouse, 1975

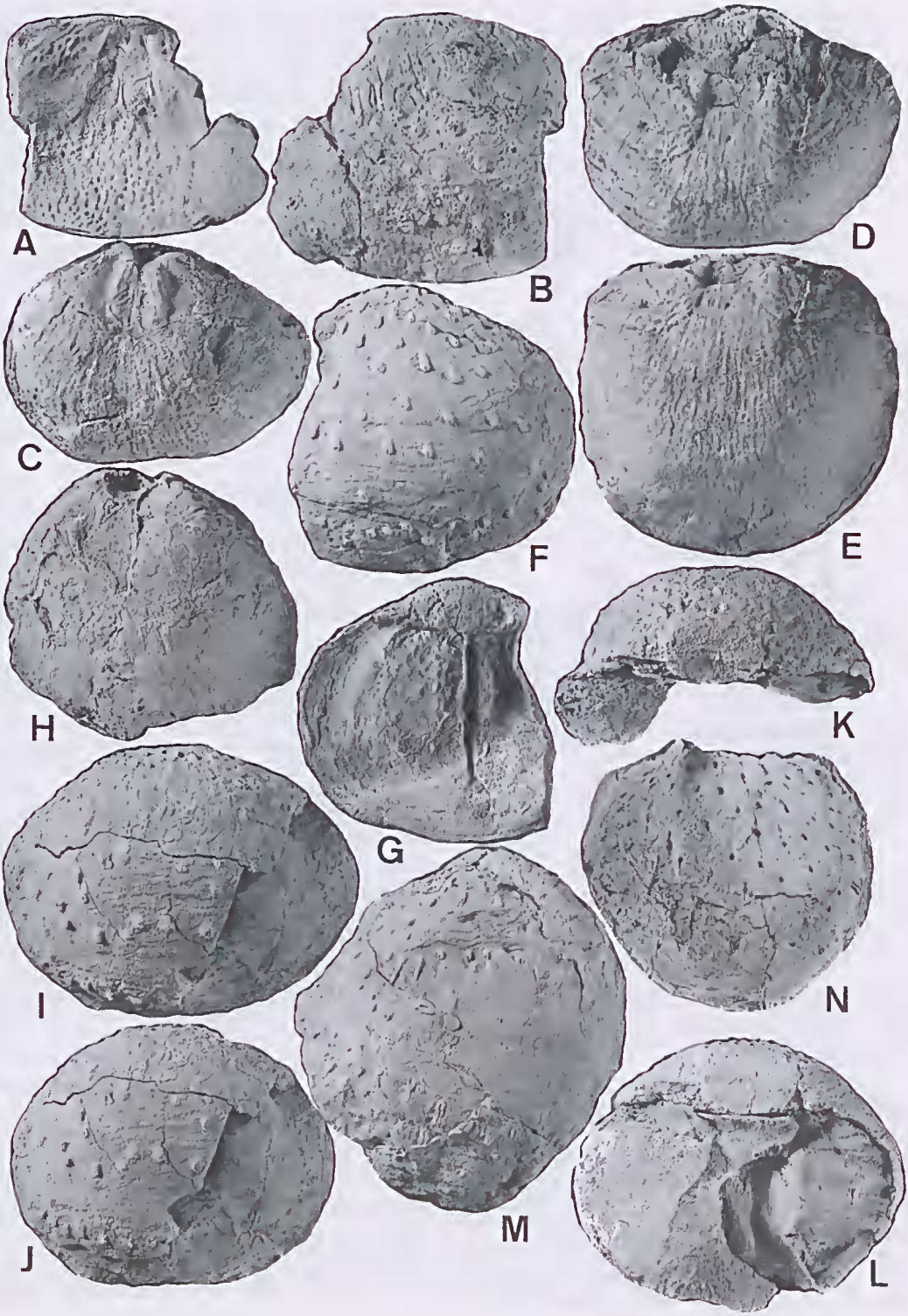
Discussion. Waterhouse (2001: 52–54) has comprehensively reviewed the use of the subordinal name Strophalosiidina. The present author ascribes the first usage of the subordinal name to Waterhouse as he was the first proposer of the subordinal rank of the group. At the very least, the date 1978 should be given for the proposal, in view of the full discussion of the subordinal content provided at that time, although the name was first published in 1975. The date 1975 has always been applied to the suborder by Archbold in his previous studies of the group (eg. Archbold 1986, 1987). As noted by Waterhouse (2001), the Brunton et al. (2000) content of the suborder is, in fact, the same as that recognised by Waterhouse (1978).

Superfamily STROPHALOSIOIDEA
Schuchert, 1913

Family STROPHALOSIDAE Schuchert, 1913

Subfamily STROPHALOSIINAE Schuchert, 1913

Discussion. Brunton et al. (2000) recognised three subfamilies within the Strophalosidae Schuchert, primarily based on the distribution of body spines.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The Strophalosiinae Schuchert were defined by only having spines on the ventral valve, the Dasyalosiinae Brunton by having spines on both valves and the Mingenewiinae Archbold by having no spines. The value of subdividing the family as proposed by Brunton et al. (2000) is not followed here because the presence or absence of dorsal spines is unlikely to be a feature of subfamilial importance although useful at the generic level (Waterhouse 1964, 1969; Clarke 1970; Archbold 1986; Briggs 1998). The Dasyalosiinae Brunton is restricted to those forms with relatively coarse, intertwining spines as suggested by Briggs (1998: 65).

Genus **Coronalosia** Waterhouse & Gupta, 1978

Type species. *Coronalosia blijtiensis* Waterhouse & Gupta, 1978.

Diagnosis. Ventral valve with relatively coarse, widely spaced body spines. Dorsal valve smooth with poorly developed pits or dimples and only rarely with radial capillae. Interior of ventral valve with striae at maturity.

Discussion. The generic name *Archaelosia* Waterhouse & Gupta (1977: 14, 1983: 125) is a *nomen nudum* which apparently refers to *Coronalosia*, a genus validly described in 1978. *Coronalosia* was accepted as a valid genus by Archbold & Singh (1993) and Brunton et al. (2000). Waterhouse (2001: 54–55, pl. 4, figs 17–21) has done much to clarify the genus and its type species. For the present study, the examination of a large suite of specimens of the type species from the Dugadda area, Garwhal Lesser Himalaya, collected by Prof. John Talent of Macquarie University, has been essential in clarifying details of the genus. *Coronalosia* is morphologically closest to *Strophalosia* King (1844), type species *Strophalosia gerardi* King (1846), but is distinguished from that genus by means of its relatively coarse, widely spaced ventral spines; essentially smooth dorsal valve exterior often with no pits or pustules and rarely with radial capillae. The ventral diductor scars of *Coronalosia* are patterned with radial striae at maturity and the radial striae continue in front of the muscle scars at maturity. The valves are thickened in gerontic individuals of *Coronalosia*.

Coronalosia argentinensis sp. nov.

Figs 3A–N, 4A–F

Holotype. DCG-MLP 356c, a mature dorsal valve.

Figured material. Three dorsal valves—DCG-MLP 356c, 356g, 356h; three ventral valves—DCG-MLP 356a, 356d, 356l; three ventral valve internal moulds—DCG-MLP 356i, 356j, 356k; one incomplete conjoined shell—DCG-MLP 356b; one ventral valve external mould—DCG-MLP 356m.

Size ranges. Maximum width, 17.5–27 mm; hinge width, 7.7–13.2 mm; ventral valve length, 13–24.5 mm; dorsal valve length, 14–17.5 mm; shell thickness, 5–9.5 mm.

Diagnosis. Small to medium sized *Coronalosia* with strongly convex ventral valve; widely spaced, subquincuncially arranged coarse ventral spines; strongly impressed adductor scars; low, thick bilobed cardinal process and thickened dorsal median septum at maturity.

Description. Shell small to medium sized for genus, transversely oval or subcircular in outline. Hinge width about two-thirds of maximum width. Convexity of ventral valve strongly developed and relatively even. No ventral sulcus but slight median flattening present. Umbo low, cicatrix often distinct. Dorsal valve gently concave. Ventral interarea low, delthyrium apparently small. Dorsal interarea low, poorly known.

Ornamentation of ventral valve consists of scattered, relatively coarse spines in subquincuncial pattern, one series only projecting at low angle, up to 1.2 mm thick at base spaced at 2 to 3 mm at 15 mm from umbo. Ears virtually absent. Growth lines weakly developed, somewhat irregular. Dorsal valve with no spines, dimples and capillae apparently absent.

Ventral interior with small teeth; adductor scars distinct, smooth, bisected by low ridge. Diductor scars large, flabellate, gently striated. Much of valve floor irregularly striate.

Fig. 3. Coronalosia argentinensis sp. nov. A, B, DCG-MLP 356d, incomplete ventral valve, internal and external views, × 3, × 3.5. C, DCG-MLP 356i, ventral valve internal mould in postero-ventral view, × 2.5. D, E, DCG-MLP 356j, ventral valve internal mould in posterior and ventral views, × 3. F, G, DCG-MLP 356b, conjoined shell in ventral and dorsal views, × 2.6, × 2.2. H, DCG-MLP 356k, ventral valve internal mould in ventral view, × 3.5. I–L, DCG-MLP 356a, ventral valve in ventral, antero-ventral, posterior and postero-dorsal views, all × 3.5. M, DCG-MLP 356l, incomplete ventral valve in ventral view, × 2.5. N, DCG-MLP 356m, ventral valve external mould, × 3.

Dorsal valve interior with strong median septum and stout, thickened bilobed cardinal process. Septum about half valve length. Adductor scars, smooth. Brachial ridges well developed.

Discussion. The new species is smaller and more strongly ventrally convex than *Coronalosia blijnensis* Waterhouse & Gupta (1978). *Strophalosia irwinensis* Coleman (see Archbold 1986: figs 1A–Z) is allied to *Coronalosia* as indicated by Briggs (1998: 66–67) and Waterhouse (2001) but is a somewhat larger species with a more gentle ventral valve convexity. Ventral spine pattern of the Western Australian, Sterlitamakian species is similar to that of *Coronalosia argentinensis*. The early Artinskian, Western Australian *Strophalosia jinbaensis* Archbold (1986; see also Archbold & Shi 1993) is also allied but is a large species with distinct dorsal dimples.

Antelo (1972: 164–167, pl. 2, figs 1–5) described specimens of a strophalosiid from Quebrada Larga, Rio Blanco, San Juan which he referred to *Heteralosia cornelliana* Derby (1872: 45–46, pl. 3, figs 28, 30, 32, 35–38; pl. 4, fig. 5; pl. 8, fig. 17; pl. 9, figs 10–11; see also reproductions of Derby's plates of brachiopods in Gonsalves 1952). Mendes (1959: 75–78, pl. 7, figs 4a–b, 5; 1961: 16, figs 19–20), transferred Derby's species from *Strophalosia* to *Heteralosia* King (1938). True *H. cornelliana* is a small species that is referable to *Heteralosia sensu stricto* or a closely related genus. The Brazilian species is comparable with small species of that genus described from the Permian of Texas (Cooper & Grant 1975). Derby's species is from the Upper Carboniferous (Pennsylvanian) Itaituba Series of the Amazon Basin, Brazil. The specimens described by Antelo (1972) are much larger than Derby's species and comparison is indicated with *Coronalosia* in view of their transversely oval outline. Illustrations of the ventral spine patterns and the dorsal valve exterior are not provided by Antelo (1972) but the dorsal valve is described by Antelo as lacking spines. Amos (1979: 75, figs a and b) refigured two of Antelo's specimens and confirmed the low nature of the cardinal process of a submature dorsal valve. Specimens collected by Dr Gabriela Cisterna and Dr Mauricio Martinez from the same locality as Antelo's material reveal ventral spines that are widely spaced, but finer than those of our species, and rare capillae on the dorsal valve but no dorsal spines. Dimples are also present on the dorsal exterior.

Genus **Tupelosia** nov. Simanauskas & Archbold

Type species. Tupelosia paganzoensis sp. nov. Simanauskas & Archbold.

Fig. 4. Coronalosia argentinensis sp. nov. A, DCG-MLP 356g, dorsal valve, internal view, × 2.6. B, C, holotype, DCG-MLP 356c, dorsal valve interior in tilted and normal views, × 3. D, E, DCG-MLP 356h, dorsal valve interior in tilted and normal views, × 3.

Diagnosis. Circular to slightly elongate Strophalosiinae with coarse recumbent ventral spines; squat, blunt internally bilobate cardinal process; dorsal septum short, about 0.3 of valve length. Ventral adductor scars deeply impressed, strongly elongate. Dorsal exterior smooth, spines absent, dimples and capillae absent. Valves strongly thickened.

Discussion. Tupelosia gen. nov. is readily differentiated from all other Strophalosiinae by its distinctive shell outline, ventral spine pattern, ventral adductor muscle scars, dorsal cardinal process and median septum. The thickened shell of *Tupelosia* at maturity recalls the shell thickening of *Coronalosia* but other morphological features such as the details of the ventral diductor scars, dorsal median septum and cardinal process are distinctive.

Tupelosia paganzoensis sp. nov.
Simanauskas & Archbold

Fig. 5A–M

Holotype. DCG-MLP 356f, a complete mature dorsal valve.

Figured material. Two dorsal valves—DCG-MLP 356f, 356n; three ventral valves—DCG-MLP 356e, 356o, 356p.

Size ranges. Maximum width, 17–18 mm; hinge width, 9–10.5 mm; dorsal valve width, 17–17.5 mm.

Diagnosis. Circular to elongate species with coarse widely scattered ventral spines. Dorsal septum short. Ventral adductor scars elongate. Dorsal exterior smooth, spines, dimples and capillae all absent.

Description. Shell circular to elongate in outline. Hinge width about 0.6 to 0.7 of maximum width. Hinge extremities rounded or finely pointed. Convexity of ventral valve pronounced, no sulcus or median flattening. Umbo small, cicatrix very small, barely recognisable. Dorsal valve gently concave. Ventral interarea low. Delthyrium small, relatively high but narrow. Dorsal interarea distinct, low, thickened.

Ventral valve exterior with scattered spines in ill-defined pattern, widely spaced. Spines in one recumbent series with distinct row close to hinge. Spines relatively coarse at base, up to 0.9 mm wide, spaced at 2 to 4.2 mm at 15 mm from umbo. Ears small. Growth lines poorly developed.

Dorsal valve lacks spines, dimples and capillae. Growth lines feebly developed. External mould of holotype lacks dorsal spines and capillae.

Ventral valve interior with pair of small, divergent teeth. Adductor muscle scars deeply impressed, smooth with growth lines, elongate and bisected by low ridge. Diductor scars large, weakly impressed, smooth and flabellate. Anterior of muscle scars valve minutely pitted, pits arranged in radiating rows.

Dorsal valve interior with short, thickened median septum, constricted and thin at base of cardinal process. Adductor muscle scars indistinct, somewhat depressed, located either side of posterior portion of septum. Cardinal process low, wide, thickened, weakly bilobed. Dorsal valve with minor internal trail developed anteriorly and laterally.

Discussion. No other known species is closely comparable in morphological details. Antelo's (1972) report of *Heteralosia coruelliana* from correlatable strata of La Quebrada Larga, Rio Blanco, San Juan indicates a comparable species to *Coronalosia argentinaensis* sp. nov. but with finer ventral spines as discussed above.

Genus **Guadalupelosia** gen. nov.
Archbold & Simanauskas

Type species. Strophalosia inexpectans Cooper & Grant (1975: 795, pl. 269, figs 13–30) from the Getaway Member of the Cherry Canyon Formation, West Texas, USA. Wordian (Kazanian).

Diagnosis. Strophalosiinae with delicate fine spines on both valves. Short, delicate rhizoid spines on ears and near umbo. Body spines delicate, recumbent over entire surface, common on ventral valve, scarcer and hair-like on dorsal valve. Delthyrium small and narrow, teeth minute and delicate. Ears small, pointed. Dorsal interarea at close to 90° to plane of valve. Ventral adductors small, distinct, with raised rims above floor of valve. Cicatrix minute. Long thin dorsal median septum extends anteriorly to marginal ridge.

Discussion. When reviewing world strophalosiinids for the present study, the occurrence of the mid-Permian, West Texas species was noted. Although assigned to *Strophalosia* by its authors, the presence of dorsal spines precludes it from that genus. In fact, the distinctive morphological features of the species preclude its inclusion in any of the known Strophalosiidae reviewed by Brunton et al. (2000). The type species of *Guadalupelosia* was well described by Cooper & Grant (1975: 795–796, pl. 269, figs 13–30) based on four specimens. The species is exceedingly rare and represents a distinctive endemic genus within the West Texas Permian. The holotype of the species is specimen USNM 151299b, well figured by Cooper & Grant (1975: pl. 269, figs 17–23). The genus is formally named by us in order to avoid confusion over the type species' generic affinities in future palaeobiogeographical studies.

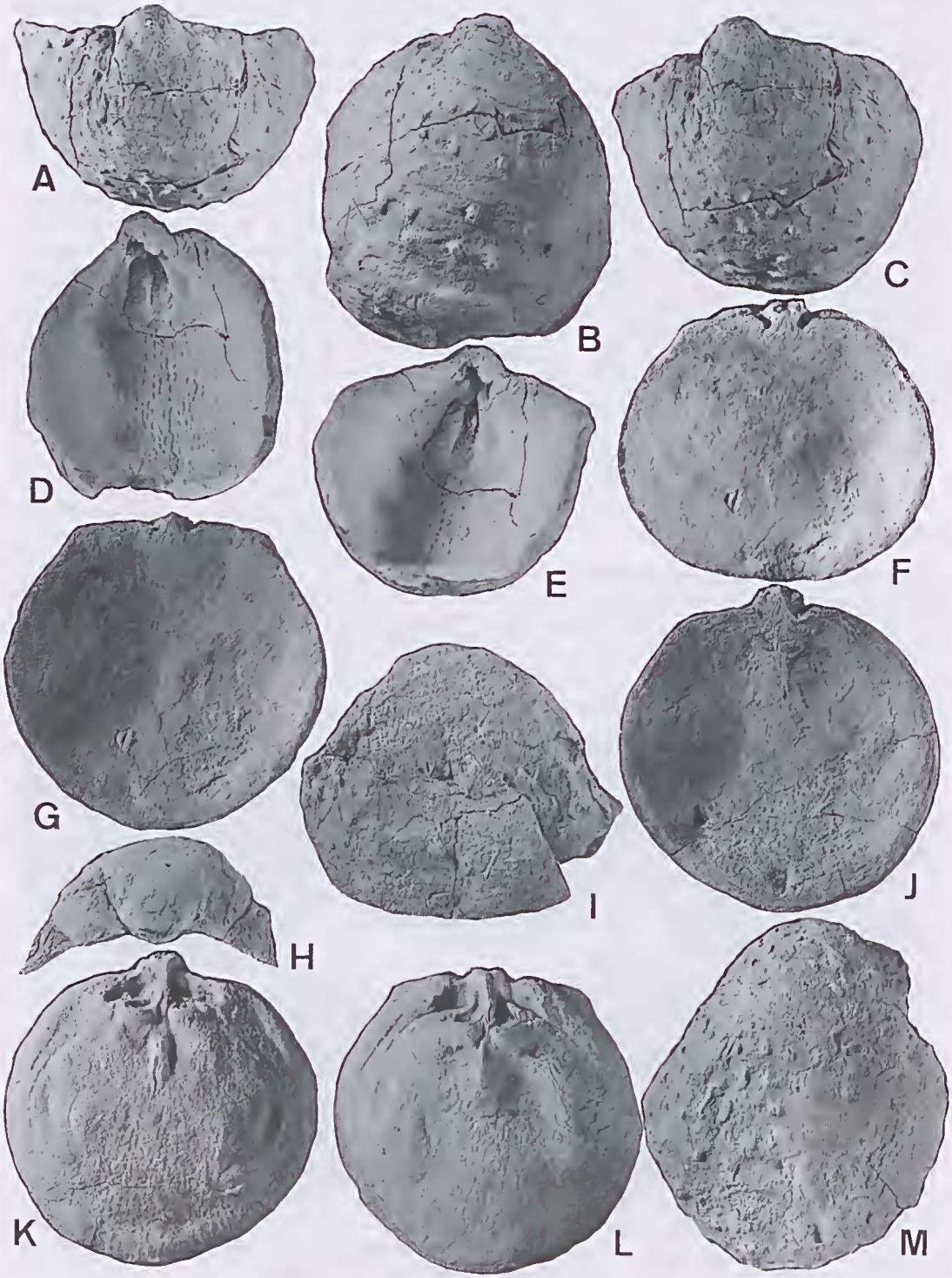
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Fig. 5. Tupelosia paganzoensis sp. nov. A–E, DCG-MLP 356e, ventral valve in posterior, ventral, and postero-ventral views, × 3, and interior and tilted anteriorly views, × 2.5. F, G, L, DCG-MLP 356n, dorsal valve in postero-dorsal, dorsal and interior views, × 3. H, I, DCG-MLP 356o, ventral valve in posterior and ventral views, × 3. J, K, DCG-MLP 356f, holotype, dorsal valve in dorsal and interior views, × 3. M, DCG-MLP 356p, ventral valve in ventral view, × 3.

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